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OBSERVATIONS ON THE DEVELOPMENT AND PARASITOIDS OF *FERGUSONINA/FERGUSOBIA* GALLS ON *MELALEUCA QUINQUENERVIA* (MYRTACEAE) IN AUSTRALIA

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Summary

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The gall-forming *Fergusonina/Fergusobia* association is being considered as a potential biocontrol agent of *Melaleuca quinquenervia* in Florida, where it has become a serious weed. This paper reports observations on the development of *Fergusonina/Fergusobia* galls on *M. quinquenervia* in coastal and sub-coastal south-eastern Queensland and northern New South Wales. The morphology of the gall and the relationship between gall size and numbers of developing cavities and insects are described. Nematodes were found in cavities containing first and second or early third stage fly larvae. Eight species of hymenopteran parasitoids were reared from galls.

KEY WORDS: Galls, field surveys, *Fergusonina*, *Fergusobia*, *Melaleuca quinquenervia*, flies, nematodes, parasitoids, gall inquilines.

Introduction

The obligate association between *Fergusonina* spp. (Diptera: Fergusoninidae) and *Fergusobia* spp. (Nematoda: Tylenchida: Sphaerulariidae) in galls on members of family Myrtaceae is amongst the most complex known (Taylor *et al.* 1996; Giblin-Davis *et al.* 2001). The fly/nematode association was first described by Currie (1937) and development of the nematode was further clarified by Fisher & Nickle (1968). The nematode has two types of life cycle, with a parthenogenetic generation followed by a heterosexual generation. In the latter, male and female nematodes develop to the adult stage in the plant gall, where young females are inseminated, and then enter the mature third stage larva of the female fly. They become parasites of the fly, growing and laying eggs in the haemolymph of the adult fly developing in the puparium. Juvenile nematodes hatch and some move into the fly ovaries. When the adult fly emerges from the gall, it deposits its eggs and juvenile nematodes within primordial leaf and flower bud tissues, where new galls develop and in which the parthenogenetic generation of the nematode occurs. Giblin-Davis (unpub. 2000) has preliminary evidence suggesting that in *M. quinquenervia* the nematode initiates gall formation before the fly eggs have hatched. The feeding activity of the fly larvae apparently leads to formation of the characteristic cavities within the gall (Currie 1937; Giblin-Davis unpub.). Associations between the nematode and fly appear to be species-specific (Giblin-Davis *et al.* 2001).

The 21 species of *Fergusonina* described from Australia are from *Eucalyptus* (Tonnoir 1937) with one species from India on *Syzygium* (Harris 1982). Most records of *Fergusobia* nematodes are from *Eucalyptus* spp. from Australia (McLeod *et al.* 1994; Giblin-Davis *et al.* 2001). Eight new species of *Fergusonina* flies, with partial descriptions of another six un-named species (Taylor pers. com. 2001) and seven new species of *Fergusobia*, with partial descriptions of another three un-named species (Davies pers. com. 2001) are currently being described from *Melaleuca*. Little is known of the biology and development of *Fergusonina/Fergusobia* galls on *Melaleuca*.

Melaleuca quinquenervia (Cav.) S. T. Blake, the broad-leafed paperbark tree, is widely distributed along coastal streams and in swamps from near Sydney to Cape York in Australia (Holliday 1989) and has become a popular ornamental tree in tropical and sub-tropical regions of the world (Gagné *et al.* 1997). It was introduced into Florida in 1906 (Schmitz *et al.* 1991) and is now regarded as the most problematic weed there (Florida Conservation Foundation 1993). It causes extensive environmental and economic damage (Balciunas & Center 1991) and has invaded more than 200,000 hectares including wetlands (Bodle *et al.* 1994). Conventional control methods, including burning, slashing and application of herbicides have proved ineffective, costly or environmentally unsound (Gagné *et al.*

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1997). In Australia, *M. quinquenervia* is associated with more than 450 herbivorous insects (Balciunas *et al.* 1995a) that suppress its growth (Balciunas & Burrows 1993) and some have potential as biocontrol agents (Balciunas *et al.* 1995a). Various gall-formers found included three species of gall midges (Diptera: Cecidomyiidae) (Gagné *et al.* 1997) and the *Fergusonina/Fergusobia* association (Balciunas *et al.* 1995b). Galls of the *Fergusonina/Fergusobia* act as a "moderately powerful" metabolic sink, and could potentially suppress seed production and reduce tree vigour (Goolsby *et al.* 2000). Hence this association is being considered among a suite of insects as biocontrol agents of *M. quinquenervia* (Balciunas *et al.* 1995b; Goolsby *et al.* 2000).

Fergusonina/Fergusobia galls on *Eucalyptus* spp. frequently contain a complex of hymenopteran parasitoid species and herbivorous lepidopteran inquilines, but there have been few studies on these associated insects (Currie 1937; Taylor *et al.* 1996). There is considerable variability between galls in terms of parasitoid populations and species and their emergence (Taylor *et al.* 1996). However, little is known about their effect on *Fergusonina/Fergusobia* galls on *Melaleuca* spp. To assess the potential of *Fergusonina/Fergusobia* spp. as biocontrol agents of *Melaleuca* spp., the role of their parasitoids needs to be examined.

This paper reports on the development of *Fergusonina/Fergusobia* galls on *M. quinquenervia* in southern Queensland and northern NSW and the parasitoids found in them, as determined from field surveys. Both the nematode and the fly are new species, and will be described elsewhere.

Materials and Methods

Galls were collected from specimens of *M. quinquenervia* in July 1997 from coastal and sub-coastal, seasonally inundated, sites in south-eastern Queensland and north-eastern New South Wales: Peregian National Park (26° 30′ S, 153° 05′ E), Coolum (26° 34′ S, 153° 05′ E), Coolum Airfield (26° 36′ S, 153° 05′ E), Roy's Road (26° 51′ S, 152° 59′ E), Morayfield (27° 07′ S, 152° 58′ E), Burpengary (27° 09′ S, 152° 58′ E), Bracken Ridge (27° 19′ S, 153° 01′ E), Nudgee (27° 23′ S, 153° 06′ E), Chelmer (27° 31′ S, 152° 58′ E), Corinda (27° 32′ S, 152° 58′ E), Pottsville (28° 22′ S, 153° 34′ E), Oxley Park (27° 33′ S, 152° 59′ E), Doolandella (27° 37′ S, 152° 59′ E), and Woodburn (29° 13′ S, 153° 16′ E). Occasional collections were also made from some of these sites in 1996, in December 1997 and July 1998.

Galls that appeared to consist of living tissue and that did not have obvious exit holes were stored in plastic bags at 5° C until examination (within 7 days). Using a scalpel blade, galls were sliced in tap water under a dissecting microscope. Large galls were cut in half and only one part was dissected. Some mature third stage fly larvae and puparia extracted were rinsed and then dissected in 0.8% NaCl for extraction of parasitic nematodes. The morphological characteristics, number of cavities, presence or absence of nematodes, number of fly larvae and/or puparia, number of wasp larvae and/or pupae, and number of lepidopteran inquilines for each gall were recorded. Nematodes were collected and fixed in hot formalin acetic acid (4:1), processed through alcohol/glycerol into pure glycerol by slow evaporation at 40° C, and mounted in glycerol on glass slides for examination (Davies & Lloyd 1996). Pupae and puparia were either preserved in alcohol or kept fresh in plastic vials and checked daily for emergence of insects. Adults emerging from galls were either preserved in 70% alcohol or pinned for identification. Undissected half galls were monitored for emergence of flies, parasitoids and inquilines and any insects emerging were treated as above.

Nematode specimens from this study were deposited in the Waite Institute Nematode Collection (WINC), accession numbers 977 - 981, 984, 985, 994 - 998. Insect voucher material was deposited in the United States Department of Agriculture, Agricultural Research Service, Australian Biological Control Laboratory (ABCL) insect collection.

Results

Description of gall

Galls (Figs 1, 2) are found throughout the year, though they are more prevalent between April and October. In particular, they occur on the flush of new vegetative growth that occurs mainly during the winter months (Goolsby *et al.* 2000). They usually develop in terminal buds (137 of 177 galls examined from 13 sites in July 1997), either on stems (89.8%) or flower spikes (10.2%), but occasionally develop as axial galls (39 of 177) or at the base of a flower spike (1 of 177). Mature galls were nodular with the appearance of a small bunch of grapes; dissections showed that each nodule contained a cavity. Those on flower spikes were sessile (Fig. 1) but terminal bud galls were stalked (Fig. 2). Some were covered with fine hairs (Fig. 2), others appeared smooth and hairless (Fig. 1).

Galls appear to have arisen from a single bud, with the ventral surface of the leaf/leaves forming the external face of the gall. Some galls, described as 'leafy galls' (Fig. 2), had the outer leaves growing as normal leaf tissue beyond the tip. When sectioned, the galled tissue was soft, except around cavities occupied by some hymenopteran inquiline larvae. In

Fig. 1.

Fig. 2.

Figs. 1 - 2. *Fergusonina/Fergusobia* galls on *Melaleuca quinquenervia*. Fig. 1. Mature flower bud gall with exit holes. Scale bar = 1 cm. Fig. 2. Leaf bud galls with leaf material growing beyond the gall. Scale bar = 1 cm.

transverse section: galls were rounded in outline and tissues frequently had a reddish or pinkish tinge. Cavities containing a developing fly larva were oval in longitudinal section and appeared to be surrounded by young, white, undifferentiated plant cells. These cells were absent in cavities containing puparia and around some cavities that contained hymenopteran inquiline larvae. Gall nodules with cavities containing puparia had a window-like area of thin plant epidermis through which the adult fly could emerge.

The average number of nodules per gall collected in 1997 was (mean ± SD) 7.6 ± 5.5 (n = 175, range 1 - 27). In July 1998, fresh weights and lengths and breadths of 33 galls from Chelmer and Corinda were measured, and the number of nodules for each gall was counted. The galls were then sliced up and the number and location of the cavities was noted. Regression analysis showed a linear relationship between the numbers of nodules and the actual number of cavities ($y = 1.8763 + 1.0353x$; $r^2 = 0.716$). The average number of nodules was 10.4 ± 5.6 (range 2 - 24) and cavities 12.6 ± 6.9 (range 3 - 28), i.e. there was an average underestimate of cavities of 18% resulting from galls large enough to contain internal cavities. One small and some larger galls contained some cavities not inside a nodule.

There was a linear relationship between fresh weight and number of cavities per gall ($y = 3.7995 + 70.04x$; $r^2 = 0.584$). Small, soft galls lacking clearly defined nodules averaged 57.2 ± 21.7 mg in weight, 5.0 ± 0.7 mm in length and 4.8 + 0.5 mm in diameter (n = 4), galls with defined nodules but lacking 'windows' averaged 119.0 ± 55.9 mg in weight, 6.3 ± 1.9 mm in length and 5.9 ± 1.6 mm in diameter (n = 12) and galls with both defined nodules and 'windows' averaged 151.0 ± 82.7 mg in weight, 7.5 ± 2.3 mm in length and 7.4 ± 1.4 mm in diameter (n = 18). Small, soft galls contained 8.7 ± 5.1 cavities (range 4 - 16), galls with defined nodules 11.7 ± 7.5 cavities (range 6 – 27) and galls with 'windows' 13.4 ± 6.9 cavities (range 3 - 28).

In December 1997, very small galls (about 3 mm diameter) referred to as 'curled leaf galls' were collected at Morayfield. Leaves growing beyond the galls were uncharacteristically small and distorted. The average number of cavities in these galls was 3 ± 1.9 (range 1 - 8; n = 10).

Number of insects per gall

The 175 galls collected from all sites and examined in July 1997 had an average of 6.1 ± 5.2 insects of all types (range 0 – 28) per gall. Seventy galls (40% of the total examined) contained more developing wasps than flies. These galls had an average of 4.0 ± 2.4 wasps per gall (range 1 - 11) and 0.8 ± 1.1 flies per gall (range 0 - 4). Eighty-six galls (49%) contained more flies than wasps, with an average of 6.2 ± 3.6 flies (range 1 - 15) and 0.7 ± 1.1 wasps (range 0 - 6) per gall. However, regression analysis showed that there was a poor relationship between the numbers of wasps and numbers of flies developing in a gall ($r^2 = 0.086$).

Thirty of these galls (17%) contained lepidopteran inquilines, usually associated with webbing and frass. Only one lepidopteran larva, from either of two undetermined species, was present in any one gall. The average number of other insects (developing flies and wasps) per gall containing a lepidopteran larva was 1.4 ± 2.0 (range 0 - 7). In 33% of the galls with lepidopteran inquilines, the larva had eaten out most of the gall and few flies or wasps survived. In one gall, six small fly larvae were found in the remaining shell of plant tissue.

Mites, psyllids and rotifers were found in or associated with galls and thrips occasionally. Other gall inquilines recorded were a coleopteran larva from one gall, and unidentified dipteran larvae from three others.

Biology of Fergusobia *associated with* Melaleuca *galls*

Nematodes were found in 54 (30.5%) galls collected from all sites in July 1997, associated with first and second stage and young third stage fly larvae. They were not found in cavities with mature third stage fly larvae, puparia, wasp parasitoids or lepidopteran inquilines. Very few infective female nematodes were collected, and then from only four galls. Examination of infective females from the galls showed that they were inseminated before entering the fly larvae. No parasitic nematodes were found from dissections of male larvae and puparia (n = 18). Female larvae contained an average of 8.3 ± 2.7 parasitic nematodes (range 3 – 11, n = 9) and female puparia 3.9 ± 2.0 (range 0 - 9, n = 15). Unexpectedly, one fly larva contained not only parasitic females but also several male nematodes. Nematode eggs were found in the haemolymph of some puparia, i.e. egg deposition began before the adult fly emerged, and newly emerged female flies contained many juvenile nematodes in the haemolymph.

Galls collected from Morayfield in December 1997 were generally earlier in development than those collected in July and mostly contained only first stage fly larvae. Nematode development was similarly at an early stage, and most of the galls examined contained only parthenogenetic females and juveniles. Of 10 galls dissected, two were parasitised by wasps and contained no nematodes. Of those containing nematodes, only two had males and these were the only galls with second stage fly larvae. The average number of parthenogenetic nematodes per cavity in the galls was 2.2 ± 0.7 (range 1 - 3, n = 8). The average total number of nematodes per cavity was 8.3 ± 5.6 (range 3 - 20).

Wasp diversity, distribution and status

In July 1997, eight species of Hymenoptera were reared from pupae dissected from 38 galls from 12 sites (Table 1). Most galls (27) contained wasps of only one species, nine galls contained two species and two galls contained three species. The wasps were *Bracon* sp. (Braconidae), *Eurytoma* sp. (Eurytomidae), *Coelocyba* sp. (Pteromalidae), *Neanastatus* sp. (Eupelmidae), *Cirrospilus* sp. (Eulophidae), *Megastigmus* sp. (Torymidae), and two unidentified species. Of these, *Eurytoma* appeared to be the most widely distributed, being reared from 16 galls at 10 sites. *Coelocyba* (from 11 galls) and *Neanastatus* (from 12 galls) were each reared from six sites, *Bracon* (from 9 galls) from five sites, *Megastigmus* (from 3 galls) from two sites and *Cirrospilus* (from 3 galls) from two sites.

Observations were made of feeding behaviour and/or emergence of particular wasps from isolated puparia. *Coelocyba* sp. emerged from a puparium dissected from a gall, i.e. it is a primary parasitoid of *Fergusonina*. *Eurytoma* sp. emerged from isolated pupae, which had developed from larvae observed feeding ectoparasitically on *Fergusonina* larvae. *Eurytoma* larvae had long, curved mandibles that were protruded for feeding. In two galls, cavities were noted which contained the remains of young second instar flies and which were connected by small 'tunnels' to other cavities containing fly and

TABLE 1. *Hymenopteran spp. reared from pupae isolated from* Fergusonina/Fergusobia *galls collected on* M. quinquenervia *in July 1997.*

Collection Site	*Bracon* sp.	*Eurytoma* sp.	*Coelocyba* sp.	*Neanastatus* sp.	*Megastigmus* sp.	*Cirrospilus* sp.	Unknown sp.
Coolum		1	1				
Coolum Airfield		1	1			1	
Roy's Road	2	2					
Morayfield				1			
Bracken Ridge	1	1	1				
Nudgee	1	3	3				
Chelmer	2	3	6	3			1
Corinda					1		
Pottsville		1			2		
Oxley Park		1		1			
Dookandella		2	1	2			
Woodburn	1	1	1	2			

Figures indicate the number of galls containing the particular insect.

wasp larvae identical to those which developed into *Eurytoma*. Fly larvae attacked by *Eurytoma* had characteristic brown marks on their cuticle, presumably resulting from wounding. Pupae that gave rise to *Bracon* sp. were encased in a loose, soft cocoon surrounded by frass, and were dissected from individual cavities. There was no evidence that they moved from cavity to cavity. Hardening of gall cells, associated with the presence of some hymenopteran inquilines, was observed in four galls.

Discussion

Given that the length of the *Fergusonina* life cycle, from egg to adult fly, is approximately six weeks (Balciunas *et al.* 1995b) and the flowering period for *M. quinquenervia* is from April to October annually, it seems likely that there are several generations of the fly per year. It remains unclear what happens to the fly over the summer period. It was not possible to determine if the small curled leaf galls collected in December 1997 contained the same species of fly found in the larger nodular galls. If they did, the fly could survive the summer and would not require a diapause.

The work described here has provided the first information on numbers of parthenogenetic female nematodes in young galls on *M. quinquenervia* but the numbers of juvenile nematodes deposited by female flies was not established. This work also has confirmed that infective female nematodes do not enter male flies (Currie 1937) but nothing is known about how they distinguish the sexes. As with *Fergusobia* species on *Eucalyptus* spp. (Fisher & Nickle 1968; Davies unpub.), infective females from *M. quinquenervia* are inseminated while in the gall. The number of female nematodes parasitic in female larvae, puparia and flies from *M. quinquenervia* is higher than for most *Fergusonina* species but the parasitic females were smaller than reported for species on *Eucalyptus* spp. (Currie 1937; Fisher & Nickle 1968; Davies unpub.).

Galls on *M. quinquenervia* are much smaller than those found on *E. camaldulensis* Dehnholm (Taylor *et al.* 1996) and contain fewer insects. This supports the suggestion (Taylor *et al.* 1996) that gall size is a reasonable estimate of resource and hence of carrying capacity of the gall.

The biology of gall associated Hymenoptera is complex and it is often difficult to determine whether a wasp is a primary parasitoid, facultative parasitoid, hyperparasitoid or inquiline (killing the resident insect and then feeding on the gall tissue) (Bouček 1988, Taylor *et al.* 1996). From studies of *Fergusonina/Fergusobia* galls on *E. camaldulensis*, Taylor *et al.* (1996) described *Coelocyba* sp. as most likely to be an inquiline or a primary endoparasitoid. Here, its emergence from a puparium from a gall confirmed its status as a primary parasitoid. *Eurytoma* is a very large genus, containing species with divergent biologies (Taylor *et al.* 1996). Here, *Eurytoma* sp. was observed feeding ectoparasitically on *Fergusonina* larvae. Pupae of *Bracon* sp. were dissected from individual cavities in galls, suggesting that this species of *Bracon* is a solitary ectoparasitoid of *Fergusonina* larvae. The occurrence of *Neanastatus* in these galls was of particular interest, because this seems to be the first record of this genus from *Fergusonina/Fergusobia* galls. Some *Neanastatus* are hyperparasitoids (Schmidt pers. com. 2001). There are several records of it from southern Queensland (Bouček 1988); it is thought to be parasitic in cecidomyiid galls.

Twelve species of Hymenoptera were reared from leaf bud galls on *E. camaldulensis* at Goolwa, South Australia (Taylor *et al.* 1996), six from flower bud galls all on *Eucalyptus* spp. in the Canberra area (Currie 1937) and four from galls on *Syzygium* in India (Harris 1982). Eight genera have been reared here from galls on *M. quinquenervia*, of which five have been previously associated with *Fergusonina*. Fewer species of hymenopteran parasitoids were associated with individual galls on *M. quinquenervia* compared to those on *E. camaldulensis* (Taylor *et al.* 1996). This may be attributable to the smaller size of the galls. In addition, in the Taylor *et al.* study galls were bagged in the field, so that all wasp species emerging were collected. Here, pupae were collected from dissected galls, so that larval stages were generally unidentified, and rare species could have been missed. Of the genera collected from *Melaleuca* galls, *Eurytoma* sp., *Coelocyba* sp. and *Bracon* sp. appear to be most widespread.

Currie (1937) concluded that parasitoids have an important role in the regulation of populations of *Fergusonina* spp. on *Eucalyptus* spp. While this study represents a short time, and gives no information about temporal variation, it confirms that when hymenopteran parasitoids and inquilines are present within galls on *M. quinquenervia*, the number of flies is often reduced. Lepidopteran inquilines often consumed the interior of whole galls, destroying both developing flies and wasps. The efficacy of *Fergusonina* in potential biocontrol programs of *M. quinquenervia* in Florida is therefore likely to be reduced by parasitism, predation and herbivory by local hymenopterans and lepidopterans. However, this may be somewhat compensated for by the oils and terpenes characteristic of *Melaleuca* (Altman 1989) which may act as deterrents to parasitism and herbivory.

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